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Forest Instability and Canopy Tree Mortality in Westland, New Zealand[1]

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ABSTRACT: Many researchers in New Zealand have accepted equilibrium models of vegetation change that assume within-stand self-replacement of the dominant tree species as the norm. Consequently, many discontinuous stand structures have been used as evidence of forest instability. For example, the patterns of regeneration and mortality in the rata–kamahi forests of Westland have led many to believe that the present canopy tree mortality is excessive. As a result, there has been considerable research on browsing by the introduced brush-tailed possum as the primary cause of the mortality. We suggest that any interpretation of this forest pattern must include a consideration of the influences on the vegetation of natural disturbances. Abundant evidence suggests that at least some of the mortality is due to senescence of cohorts of trees that originated at approximately the same time after events such as windthrow and mass movements. It may be that browsing by possums hastens the death of trees already susceptible as a result of natural stand development processes.

EQUILIBRIUM MODELS OF vegetation change were widely accepted in New Zealand in the past. These assumed long-term site stability and postulated gradual vegetation change culminating in a self-maintaining community variously referred to as a steady-state, equilibrium, or climax community. An example of such a model is the classical successional theory developed by Clements (1916) and others in the early part of this century in which vegetation change is regarded as unidirectional and deterministic. Since succession to climatic climax was at least theoretically accepted in New Zealand as a valid concept, within-stand self-replacement by the dominant tree species was considered the norm. According to this concept of equilibrium in vegetation change, the apparent lack of all-aged populations in many stands could be regarded as evidence of forest instability. Many reasons were offered for such instability; perhaps the two most common were recent climate change (Holloway 1954, Wardle 1963) and the effects of introduced browsing animals.

The climate change hypothesis has been reviewed elsewhere (Burrows and Greenland 1979, Molloy 1969), and alternative explanations for discontinuous population structures have been given for several of the conifer species concerned (Clayton-Greene 1977, McSweeney 1982, Veblen and Stewart 1982*a*). Many discontinuous population structures can be explained by consideration of the regeneration ecology of the species themselves, and a more appropriate conceptual framework for interpreting vegetation change in these forests may be a kinetic scheme (Drury and Nisbet 1971, Veblen and Stewart 1982*a*). A similar argument was presented by Ogden (1976, 1980), who pointed out the dangers of assuming a climatic explanation

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for stand structures that may have arisen solely through stand dynamic processes.

The effects of browsing animals have also been used to explain deviations from all-aged population structures. However, in many areas, factors other than browsing have had an influence on forest structure (Veblen and Stewart 1980, 1982*b*). This is especially true in the rata–kamahi forests of Westland, where observed patterns of mortality and regeneration need to be thoroughly investigated before the present population structures are interpreted. Any future investigation should therefore include a consideration of the major tree species' regeneration ecology as well as an understanding of the dynamics of the stands in which they occur. In contrast to many of the previous studies on tree mortality in Westland that concentrated on browsing of the introduced brush-tailed possum as the primary cause of mortality, we emphasize the importance of considering many possible factors, including the effects of natural disturbances.

While the influences on the vegetation of possum browsing have been the subject of considerable debate, the importance of other types of disturbance in regeneration has perhaps been overlooked. Natural disturbances such as vulcanism, fire, violent wind storms, and mass movements have been frequent occurrences in the New Zealand postglacial environment (Molloy 1969). Influences on the vegetation resulting from such disturbances may be subtle, such as the replacement of several canopy trees after minor windthrow, or may be more obvious, such as the extensive damage caused by the 1936 storm in the North Island (Thomson 1936). Disturbances affecting the vegetation in Westland include: windstorms; temperature fluctuations; precipitation variability; fluvial erosion, deposition, and flooding; coastal erosion, deposition, and dune movement; mass movements and biotic disturbances (browsing animals, insects, and disease outbreaks). Given the present frequency and visual extent of these disturbances, the vegetation *must* have also been significantly affected in the past. However, few studies have given major emphasis to disturbances other than those relating to the climate change hypothesis or to the effects of browsing animals (and human disturbance). This may be due, in part, to the scanty disturbance record in many locations and the difficulty of interpreting major events that occurred in the distant past. With collaboration among scientists of different disciplines, however, it may be possible to resolve some of these problems. For example, the high erosion rates in the Ruahine Range in the North Island have been believed to be significantly exacerbated by the effects of browsing animals; however, in a recent geomorphological study, Mosley (1978) considered that most of the erosion could be explained by natural erosional processes and the youthful nature of the range. Every possible factor that may influence forest dynamics should be taken into consideration.

FOREST MORTALITY IN WESTLAND

In many forested areas in Westland, the main canopy tree species, particularly southern rata (*Metrosideros umbellata*) and kamahi (*Weinmannia racemosa*), appear to be dying in large numbers. Mortality often appears to be synchronous, with many trees in a single patch affected, or may involve only single trees. The cause of this widespread mortality has been the source of considerable debate but is thought to be the result of browsing pressure from rapidly expanding populations of the introduced possum (Pekelharing 1979). However, several salient points conflict with this interpretation (Stewart and Veblen 1982*b*). The first, and perhaps most important, point is that mortality of the canopy dominants (as documented by old photographs and historical records) was evident in these forests before the buildup of animal numbers (Holloway 1957, Morgan 1908). Second, many of the patches of dead trees are not the broad-leaved rata and kamahi, but are coniferous trees such as mountain cedar (*Libocedrus bidwillii*) and Hall's totara (*Podocarpus hallii*). The palatability of these coniferous species is generally regarded as low (Coleman, Gillman, and Green 1980, Fitzgerald and Wardle 1979). All sizes of trees are not similarly affected by the mortality; young trees appear to be little affected and most mortality is in stands of large trees. Senescent stands are commonly found on steep slopes in Westland and often appear to be even-aged (Holloway 1957, Stewart and Veblen 1982*a*, Wardle 1980). Verification of even age is required, but there is abundant evidence for the regeneration of rata and kamahi on bared slopes after mass movements and windthrow, which appears to result in even-aged stands (Stewart and Veblen 1982*a*).

As early as 1955, researchers were aware that factors other than possum browsing were important in the mortality. An extensive unpublished report produced by scientists from several government departments in 1955 contains references to some of these factors (summarized in Stewart and Veblen 1982*b*). Briefly, they considered that other important aspects and observations related to the mortality included: (1) Old and overmature trees are more susceptible to various physical and biotic disturbances such as wind storms, soil movement, drought, insect attack, or possum browsing; (2) tree mortality also may be due to other factors such as loss of root hold on steep slopes and competition; (3) browsing animals may have indirectly affected tree health by disturbing soil and litter layers and by reducing native insectivorous bird populations through changing their habitat, resulting in increases in insect populations; (4) past climate change may have increased the susceptibility of relic rata stands to damage from browsing animals (Holloway 1954); and (5) apparently healthy stands often were infested with possums. Although the complexity of the problem was realized early in the assessment of the causes of the mortality, much of the subsequent work has concentrated on the effects of possums.

ROLE OF POSSUMS IN THE MORTALITY

Evidence from several areas of possum research has been used to implicate possums as the cause of tree death. Studies of possum diet have shown that rata and kamahi can form a large proportion of the foliage eaten by possums (Coleman, Gillman, and Green 1980, Fitzgerald and Wardle 1979). Other studies have implicated possums from observed patterns of mortality, signs of possum presence and browse, and possum behavior (Holloway et al. 1963, McKelvey 1959, Wardle 1974), and from the apparent coincidence of increasing tree mortality with the spread and buildup of possum populations (Pekelharing 1979).

Many of these studies rely on circumstantial evidence and as such are subject to differences in individual interpretation. The circumstantial evidence for possums as a cause of mortality could also be used in alternative explanations. For example, the coincidence of high densities of possums with areas of high mortality of canopy trees has often been used to implicate possums as the cause of the mortality. However, in these areas there is often wide diversity of understory shrubs, small trees, herbs, and ferns, and this may attract high numbers of possums. Another explanation, therefore, is that the possums may or may not be a cause of mortality but are attracted to the area by the increased diversity of diet (Veblen and Stewart 1982*b*). The interpretation of browse and dietary information is also problematic. Studies that compare the amount of a species eaten (from stomach contents or fecal analysis) with its availability in the vegetation have to select an appropriate measure to estimate the total biomass available for browse. For example, a high component of rata in the diet (as measured from fecal analysis) may not necessarily reflect heavy browsing pressure on this species, because the total amount of rata biomass available in old-growth stands may be many times that of all the shrub and small tree species combined. Conversely, a small percentage of a species such as *Schefflera digitata* in the diet might reflect heavy pressure on this small tree owing to its much less abundant foliage.

The large amounts of rata and kamahi eaten by possums does provide a possible mechanism for explaining the extensive tree mortality in Westland rata–kamahi forests. However, the problems in this interpretation are also confounded by the lack of knowledge of how much mortality to expect in the absence of browsing animals; this is particularly difficult to assess since most areas of mainland New Zealand have now been colonized by possums.

CONCLUSIONS

We conclude that although possums may often be implicated as the immediate cause of death of individual trees, they cannot be considered the *sole* cause of all mortality. The many mechanisms that contribute to the observed patterns of regeneration and mortality include disturbance and natural stand dynamics as well as browsing by possums and other deleterious influences. The biotic agents responsible for immediate tree death may only be triggers to mortality and not underlying causes. Thus, in our interpretation, the synchronous senescence of the trees is an essential contributory factor to the mortality. We therefore emphasize the importance of natural stand dynamic processes involved in the creation of cohorts of trees that are likely to senesce at a similar time. It is likely that possum browsing may make the mortality more coincident than it would be naturally, since browsing often appears to be the immediate factor that hastens the death of the trees.

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